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THE VISUAL ACUITY OF THE CORAL FISH

MICROCANTHUS STRIGATUS (CUVIER & VALENCIENNES)[1]

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With 16 Tables and 10 Text-figures

CONTENTS

I. Introduction

In angling, fine and transparent fishing line is used to render the drail invisible against the bright water background. This proves without a doubt that fish have a keen sight for external objects. Some fish have indeed relatively large eyes in contrast to their size (Fig. 1). In Japan fine and transparent thread made from the silk gland of the Japanese oak-worm moth is used instead of catgut. Recently, drail made from nylon has also been used. Fine drail made from wild-cocoon silk above mentioned is 0.08 mm in diameter. Whether such fine drail could be seen by fish or not, will be discussed below in VII (Interpretation).

After the pioneer works of HERTER (1929, 1930) on the form perception of fish, BRUNNER (1934) studied the visual acuity of the fresh water fish, *Phoxinus laevis* (Erlitze), by a training method. In his study the limit of visual acuity was determined by training fish to select a fine parallel striped pattern ($+$) against a gray paper ($-$) in different light intensities. In this study the coral fish *Microcanthus*

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strigatus (belonging to Scorpididae) with large eye was adopted as the material.   The fish was trained to select one of either a vertically or horizontally striped pattern on the simultaneous presentation of these two figures in water (Fig. 3).   This fish showed a keener sight than the Erlitze, as the former has larger eyes than the latter so much, so that the eye axis length of the former is 8 mm, while that of the latter is 2 mm (BRUNNER, 1934, p. 313).

This study was undertaken during the warm seasons of 1936 and 1937 at the Seto Marine Biological Laboratory of Kyoto University.   The preliminary report on the subject has been published in

The visual acuity of fish (in Japanese).   Zool. Mag., vol. 48, p. 203, 1936.

Fig. 1. *Microcanthus strigatus.* Scale in cm.   ×1

II. Method

The fish used for experiment was the coral fish *Microcanthus strigatus* (CUVIER et VALENCIENNES), in Japanese called "Kagokakidai."   The fish has a body length of about 20 cm in full growth, and has seven dark colored striations along the body axis on a lemon yellow background (Fig. 1).   Fish having a body length of from 9 to 11 cm were chosen for the experiment.

Each fish was kept alone in a wooden aquarium of the size 72.5 cm (length), 27.3 cm (width) and 24 cm (depth).   The water level was kept 16.5 cm from the bottom (Fig. 2).   On one end of the aquarium two rectanglar figures of 2.5×2.5 cm were simultaneously presented in sea water, each separated 5 cm apart by black painted wooden board (Fig. 3 A).   Behind the figure a small piece of cooked lobster
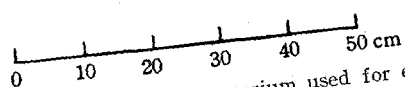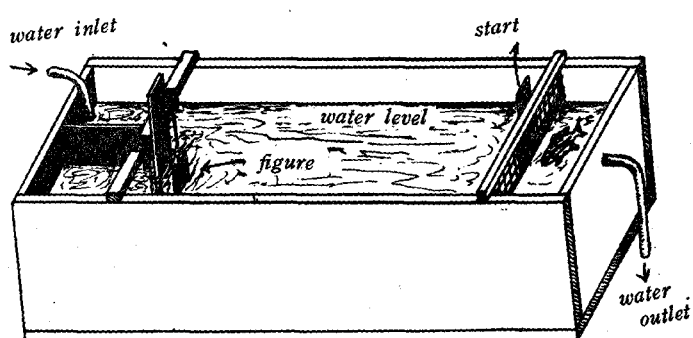
The Visual Acuity of the Coral Fish

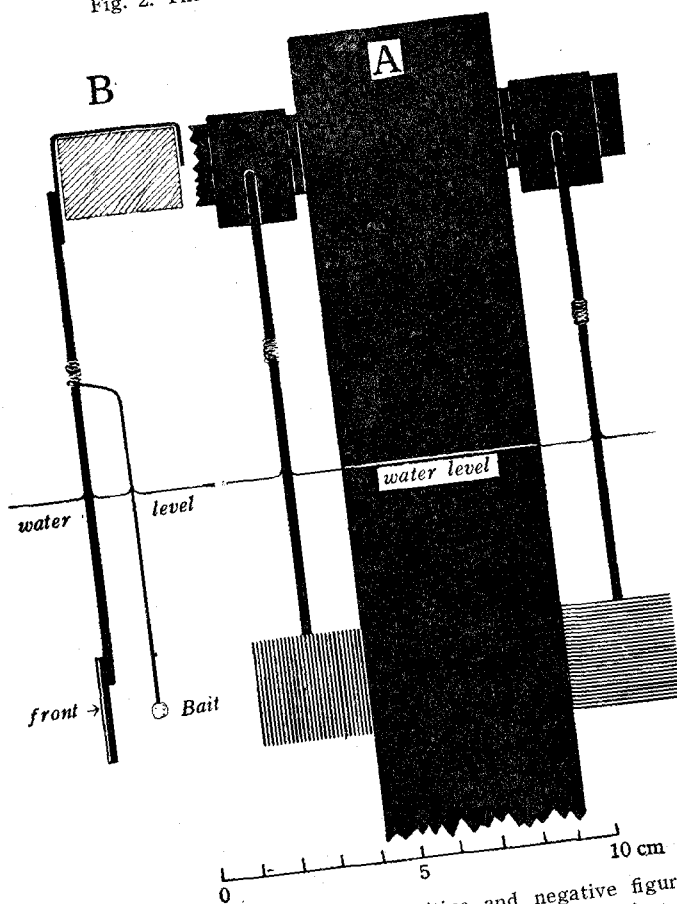Fig. 2. The aquarium used for experiment.

Fig. 3. Arrangement of positive and negative figures. A is the frontal view, and B the side view.

meat was attached as bait to the end of a wire ; one piece was loosely attached behind the positive figure while the other was firmly fastened by melted paraffine behind the negative figure (Fig. 3B). In training, the fish was confined in the starting chamber at the other end of the aquarium, and then the metal plate on the entrance of the chamber was raised. The fish dashed to the figure and tried to obtain the bait on the back side of the figure. At first rough striped figures were used as training figures, and when these patterns were mastered in selecting correct figure (one of the horizontally and vertically striped figures), a finer striped figure was presented for further training. In testing, the bait was loosely attached for both figures. This method was, however, by no means absolutely good. If the fish once had learned to select bait by figural difference, this method was excellent. If the fish had once learned to take eatable bait not by figural difference but by a difference in the bait itself, further training was totally in vain. An unclever fish, so to speak, deceived by the experimental mechanism, yielded desirable results for the experimenter. In the course of training some fish showed occasionally the tendency to select the figure repeatedly from one definite side of the aquarium independently of the difference of figural pattern. Therefore the position of the two figures should have been changed at random in each trial of training or in the test.

Table 1. Width of black and white stripes.

No. of figure	Number of black lines in 25 mm	Number of black and white lines in 10 cm	Width of black or white lines in mm
1	1	10.94	9.14
2	2	18.08	5.53
3	4	27.88	3.59
4	5	36.62	2.73
5	7	51.28	1.95
6	10	71.43	1.40
7	13	95.50	1.05
8	19	137.9	0.73
9	22	160.0	0.63
10	27	172.2	0.52
11	33	239.8	0.42
12	40	298.5	0.34
13	57	420.0	0.24
14	82	611.1	0.16
15	107	789.0	0.13
16	135	1000	0.10
17	165	1209	0.083
18	196	1429	0.077
19	228	1667	0.060
20	270	1964	0.051

Preparation of the figures. 263 equidistant parallel lines were engraved with a diamond pencil on a rectanglar bronze plate (93×93 cm) ; and this bronze grating was printed on paper. The printed striped pattern was reduced by photograph to the desirable magnitudes. The figures of 2.5×2.5 cm used in this experiment were made from the printing of the negatives thus prepared (Figs. 14—20 in Table 1). The figures of rougher stripes (Figs. 1—13 in Table 1) were prepared by photography from carefully handdrawn equidistant parallel lines on drawing paper.

III. Visual Acuity

a. Minimal physiological visual angle

The training of fish to discriminate the horizontally and vertically striped figures was started at first with relatively roughly striped figures. In many cases it was began with the figure No. 9 described in Table 1 (width of black or white stripe 0.4 mm). When the training was proved to be completed by test, further training was continued with the finer patterns (No. 12, 14, 16, 18 and finally 20). When the finer figures were first presented, the fish could not discriminate them at first. Further training was required to master the new condition.

Under day light or under bright incandescent illumination, the limit of the fineness of parallel striation discriminated by the fish lay between figures No. 18 and No. 20 (width of black or white striation 0.077 mm and 0.051 mm respectively).

Relation between visual acuity and illumination. The experiment to determine the above relation was accomplished under conditions of varied illumination. From 0.1 to 423 Lux illuminated conditions were prepared by electric lamp arrangement. The upper and four sides of the aquarium were surrounded by thin and opaque paper to diffuse the electric light from above. The result is presented in Table 2 and in Fig. 4.

The curve plotted in Fig. 4 indicates clearly the role played by the cones in vision under illumination brighter than 5 Lux. Under illumination below 0.4 Lux the rods seems to play the principal part in figural discrimination. In the transitory phase under illumination between 5 and 0.4 Lux, the vision would depend on both the cones and the rods.

Calculation of the physiological visual angle based on experiment. The visual angle may be calculated by the minimal width of striation discriminated and the eye distance from the figure when the fish has seen the object distinctly. Of course the distance of discrimination is dependent on the width of striation. The coarse pattern may be discriminated at a greater distance than the finer ones. However, it is a well known fact that fish are normally myopic. As Tables 3 and 4 indicate, the fish sees the object at a definite distance from the figures relatively independent of the width of striation. At the point of apparent discrimination of the two figures, the course of swimming turned to one of the two figures. The distance of this turning point of

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Table 2. Minimum width (d) of parallel stripes discriminated by four fish
(No. 6, 1, 2, 4) under different illuminations.

| Illumination I in Lux	$\log I$	Width (d) of stripe in mm				Mean d in mm	$1/d$	Visual angle $d/40$ mm
		No. 6	No. 1	No. 2	No. 4			
423	2.63	0.051	0.051	0.051	0.077	0.058	17.4	4′59″
282	2.46	0.051	0.051	0.051	0.077	0.058	17.4	4′59″
104	2.02	0.083	0.083	0.077	0.100	0.086	11.6	7′25″
39.6	1.60	0.164	0.127	0.164	0.237	0.146	6.85	12′43″
11.0	1.04	0.237	0.164	0.164	0.237	0.201	4.98	17′
5.0	0.70	0.237	0.237	0.237	0.237	0.237	4.22	20′
2.2	0.34	0.237	0.237	0.237	0.237	0.237	4.22	20′
0.4	−0.40	0.237	0.237	0.237	0.237	0.237	4.22	20′
0.3	−0.52	0.335	0.335	0.335	0.335	0.335	2.99	30′
0.1	−1.00	0.417	0.417	0.417	0.417	0.417	2.39	36′
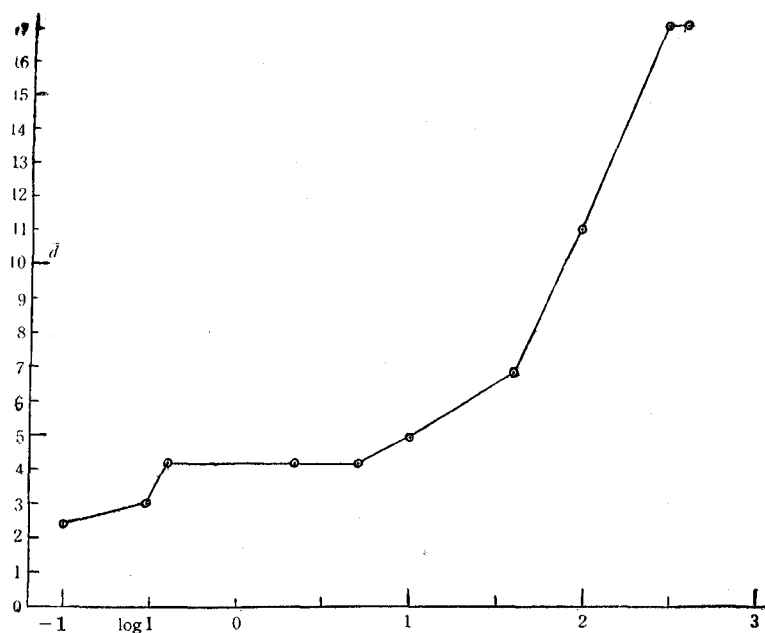
Fig. 4. The relation between visual acuity $(1/d)$ and illumination. Plotted
from the data in Table 2.

Table 3. The number of cases in which the fish apparently discrimitated the simultaneously presented figures at different distances. Under illumination lower than 11 Lux.

Distance from figure in cm	No. of figure and the width of striation in mm										Sum
	No. 11 0.42 mm	No. 12 0.34	No. 13 0.24	No. 14 0.16	No. 15 0.13	No. 16 0.10	No. 17 0.08	No. 18 0.07	No. 19 0.06	No. 20 0.05	
1	—	—	—	—	—	—	—	—	—	—	0
2	1	—	—	—	—	1	—	—	—	1	3
3	4.5	1	2	—	—	1	5	4	—	1	18.5
4	9.5	3	7	1	1	—	8	13	3	8	53.5
5	6	2	9	1	—	1	4	5	5	11	44
6	1	1	15	1	4	7	8	5	2	7	51
7	1	—	1	—	1	—	—	3	—	1	7
8	—	1	—	1	2	3	3	3	—	3	16
9	—	—	—	—	—	2	—	4	—	1	7
10	—	—	—	3	3	2	—	8	—	1	17
11	—	—	—	—	1	—	1	—	—	1	3
Mean distadce in cm	4.3	4.9	5.2	7.6	7.7	6.7	5.2	6.2	4.9	5.6	

Table 4. The number of cases in which the fish apparently discriminated the simultaneously presented figures at different distances.

Distance from figure in cm	Under illumination lower than 11 Lux	Under illumination higher than 100 Lux	Total sum
1	—	—	0
2	3	1	4
3	18.5	23	41.5
4	53.5	116	169.5
5	44	94	138
6	51	77.5	128.5
7	7	67	74
8	16	31.5	47.5
9	7	53	60
10	17		
11	3	100	120
12	—		
14–16	—	38	38
18–20	—	22	22
25	—	21	21
30	—	18	18
35	—	3	3
40	—	9	9
Sum	220	674	894

swimming course and the distance of to and fro swimming plane before the figures indicated the distance of distinct discrimination of the two figures. There were several cases in which the fish discriminated the coarse striped pattern at a distance of 40 cm, but these were rather exceptional. In most cases the discrimination was made at 4 cm from the figures as Tables 3, 4 and Fig. 5 indicate. The visual angle (ω) is calculated by $\omega = \dfrac{\text{minimal width of striation}}{\text{distance of distinct discrimination}}$. As indicated in Table 2, fish No. 6, 1 and 2 discriminated figure No. 20 (width of single stripe 0.051 mm), then

$$\omega = 0.051 \text{ mm}/40 \text{ mm} = 0.001275 = 4'23'' \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots (1)$$

The average width of striation discriminated by four fish in Table 2 was 0.058 mm then

$$\omega = 0.058 \text{ mm}/40 \text{ mm} = 0.00145 = 4'59'' \qquad \cdots\cdots\cdots\cdots\cdots\cdots (2)$$
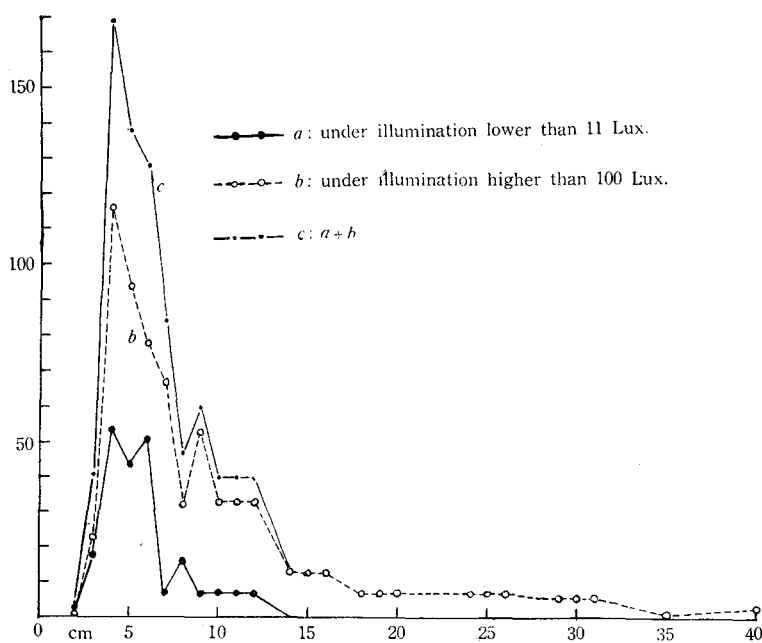
Fig. 5.   The frequency of cases in which the fish apparently discrimin-
ated the two figures.

b. Minimal morphological visual angle

The morphological visual angle may be gotten by knowing the mean cone distance in the retina, the refraction index of the sea water and the total refraction index of the lens.

1) *Mean distance of cones in the retina.*   The cones are distributed regularly in the retina, but they are not equidistant. As the direct measurement of their distances

from each other in microscopic preparation was extremely difficult, it was assumed that the cones were arranged equidistant to each other, or that they were distributed in the center of minute regular hexagon. If a is the side of the regular hexagon, its area is

$$3\sqrt{3}/2 = a^2 \quad \dots\dots\dots\dots\dots\dots\dots(3)$$

If d is the distance of the two centers of the adjacent hexagon, the distance (d) of each cone is

$$d = \sqrt{3}\,a \quad \dots\dots\dots\dots\dots\dots\dots(4)$$

In the microscopic preparation of the retina dissected parallel to the retinal surface, the number of cones was counted in the rectanglar area of $93 \times 93\mu$. The area of one cone in the area of $\overline{93\mu}^2$ containing n cones was $(m = 93\mu)$

$$\frac{m^2}{n} = \frac{3\sqrt{3}}{2}a^2 \quad \text{or} \quad a = \sqrt{\frac{2}{3\sqrt{3}}} \cdot \frac{m}{\sqrt{n}} \quad \dots\dots\dots\dots(5)$$

From (4) and (5)

$$d = \sqrt{3}\,a = \sqrt{\frac{2}{\sqrt{3}}} \cdot \frac{m}{\sqrt{n}} = \frac{93}{\sqrt{n}} \cdot \sqrt{\frac{2}{\sqrt{3}}} \quad \text{or} \quad d = \frac{99.93}{\sqrt{n}}\mu \quad \dots\dots(6)$$

From this relation, if the number n of cones in $\overline{93\mu}^2$ is known, the mean distance of cones in the retina can be estimated. If $n = 140$ (Table 7)

$$d = 99.93/\sqrt{140} = 8.4\mu \quad \dots\dots\dots\dots\dots\dots\dots(7)$$

2) *Calculation of the total lens refraction index* (n_2). MATTHIESSEN (1886) gave the value of n_2 as 1.6763 in codfish and 1.6476 in carp. The precise value of n_2 should be measured for each species of fish. In determining the total lens refraction index of *Microcanthus strigatus*, the following relation for the spherical lens system is expected (HOUSTOUN 1924, p. 44):

F: focal distance of lens
r: radius of lens
n_1: refraction index of the sea water (1.339)
n_2: total refraction index of lens (unknown)
m: length of eye axis $(F + r)$

$$F + r = r \cdot \frac{n_2}{2(n_2 - n_1)} + r = r \cdot \frac{3n_2 - 2.678}{2(n_2 - 1.339)}$$

$$r \cdot \frac{3n_2 - 2.678}{2(n_2 - 1.339)} = m, \quad \text{or} \quad n_2 = \frac{2.678(m - r)}{2m - 3r} \quad \dots\dots\dots\dots(8)$$

From the direct measurement of r and m as indicated in Table 5, $m - r/2m - 3r$ was calculated for fish 3—17 cm long. This value was practically constant (0.623). From (8)

$$n_2 = \frac{2.678(m - r)}{2m - 3r} = 2.678 \times 0.623 = 1.668 \quad \dots\dots\dots\dots(9)$$

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Table 5. Calculation of the total refraction index (n_2) of the
fish eye from the radius of lens (r) and the axis of the eye

(m) ; $n_2 = \dfrac{2.678(m-r)}{2m-3r} = 2.678 \times 0.623 = 1.668.$

Body length in cm	Mean length of the radius of lens (r) in mm	No. of specimen	Mean length of the axis of eye (m) in mm	No. of specimen	$m-r$ in mm	$2m-3r$ in mm	$\dfrac{m-r}{2m-3r}$
4– 5	1.18	2	4.07	2	2.89	4.60	0.627
5– 6	1.22	6	4.35	6	3.13	5.04	0.620
6– 7	1.36	7	4.67	5	3.31	5.26	0.629
7– 8	1.52	1	5.50	1	3.98	6.44	0.620
8– 9	—	—	—	—	—	—	—
9–10	2.09	7	7.60	3	5.54	8.93	0.620
10–11	2.26	7	7.95	1	5.69	9.12	0.640
11–12	2.49	2	—	—	—	—	—
12–13	2.52	2	9.13	2	6.61	10.70	0.618
13–14	2.70	5	—	—	—	—	—
14–15	3.23	1	—	—	—	—	—
15–16	3.34	1	11.80	1	8.46	13.58	0.623
16–17	3.55	3	12.10	1	8.55	13.55	0.631
						Mean	0.623

3) *Relation of minimal physiological and morphological visual angle.*

    ω : minimal visual angle measured by experiment (0.001275 or 4′ 23″)

    ω' : morphological visual angle

    n_1 : refraction index of the sea water (1.339)

    n_2 : total refraction index of lens (1.668)

then $\omega' = \dfrac{n_1}{n_2}\,\omega = \dfrac{1.339}{1.668}\,\omega = 0.80\,\omega$ From (1) $\omega = \dfrac{0.051\ \text{mm}}{40\ \text{mm}} = 0.001275$ or 4′ 23″ then

$$\omega' = 0.80\,\omega = 0.80 \times 0.001275 = 0.00102 \quad \text{or} \quad 3'\ 30'' \qquad \cdots\cdots\cdots\cdots (10)$$

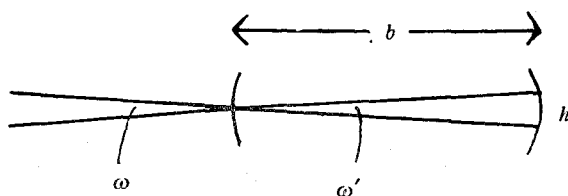From Fig. 6, $h = b\,tg\omega' = b\omega'$, $(tg\omega' = \omega')$

Fig. 6. The schema of the optical system of the eye.

For fish with body lengths of from 10—11 cm, the length of eye axis was from 7.60
to 8.40 mm, or 8 mm in average value by direct measurement.

From (10) $$h = b\omega' = 8.00 \times 0.00102 \text{ mm} = 8.2\mu \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots (11)$$

4) *Calculation of morphological visual angle from the mean cones distance.* From Table 7 the mean number of cones (n) contained in $\overline{93\mu}^2$ area in the central and back parts of the retina of fish with body lengths of 10—10.8 cm was 140. The mean distance of cones is given as already mentioned in (6).

$$d = \frac{99.93}{\sqrt{n}} \mu = \frac{99.93}{\sqrt{140}} \mu = 8.4 \mu$$

The value of d based on experimental data was 8.2μ (11) and the value calculated from the mean cone distance was 8.4μ as above mentioned. Both values practically coincide, allowing the high probable error in experiment and measurement in this type of work.

The minimal morphological visual angle may also be calculated by the length of eye axis and the mean distance of cones as follows:

$$\omega' = 8.4\mu / 8 \text{ mm} = 0.00105 \quad \text{or} \quad 3' \, 36'' \quad \cdots\cdots\cdots\cdots\cdots (12)$$

$3' \, 36''$ is not a very different value from the $3' \, 30''$ theoretically deduced from minimal physiological visual angle (10).

IV. Distribution of Cones in the Retina

Fish retina was fixed in an alcohol-formalin mixture (2 parts 80% alcohol plus 1 part 40% formaldehyde after PETERFI), and the fixed retina was dissected by microtome after paraffine imbedding. Section was made parallel to the retinal surface. 9 parts of the retina were chosen for dissection as indicated in Fig. 7. Microtomic sections
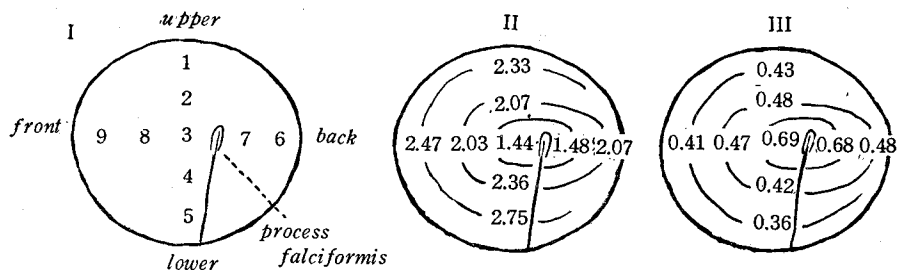
Fig. 7. The retina of *Microcanthus strigatus* enlarged.
  I. 9 parts of the retina dissected.
  II. The ratio of the number of cones/ganglion cells as indicated in Table 10.
  III. Reciprocal of the above as in Table 10.

were stained by HEIDENHEIN's hematoxylin and eosin. The cones were stained pink red, and the ganglion cells blue violet. The number of cones and ganglion cells were counted in an area $93 \times 93\mu$. In Table 6 is presented the number of cones in 9 parts of the retina of this fish with body lengths from 9.4 to 16.5 cm.

Table 6. The number and the mean distance of cones in the area of $\overline{93\mu}^2$ in the different sections of retina.

Specimen	Body length in cm	Part of the retina									Mean number	Mean distance in μ
		1	2	3	4	5	6	7	8	9		
C	9.4	76	93	156.6	90.5	100	141.5	171.5	80	114	113.5	9.4
b	10	61	80.5	134.5	87.5	96	136	175	121	91	109.2	9.6
i	10.3	66	67	120.5	81	80	141.5	100	99	94	94.3	10.3
B	10.4	58	79.5	163	77	72.5	182.5	157.5	86	87.5	85.9	10.2
d	10.4	64	74.5	137	85	96.5	147	162	101	124	110.1	9.5
k	10.8	70.8	62	102	83.5	79	128	128	85	81	91	10.5
W	10.8	67.5	54	107	73	73.5	119.5	100.5	102.5	84.5	86.9	10.7
Mean number of cones		66.2	72.9	131.5	82.5	85.4	142.3	142.1	96.4	96.6	100.1	
Mean distance of cones calculated from $\dfrac{99.93}{\sqrt{n}}$ in μ		12.2	11.7	8.7	11.0	10.8	8.4	8.4	10.2	10.2		10.0

Specimen	Body length	1	2	3	4	5	6	7	8	9	Mean number	Mean distance
3	12.3	50.5	54.5	136.5	60.5	62.5	82.5	88	68.5	63	74.1	11.6
4	13.0	45	52	102.5	64	51	86.5	122	83.5	69	75.1	11.5
n	13.6	46.8	57	79.5	53.3	59	110.3	106	75.5	80.5	74.3	11.6
m	13.9	43.5	42.5	95	49	74	83	89.5	82.5	63	69.1	12.0
Mean number of cones		46.5	51.5	103.4	56.7	61.6	90.6	101.4	77.6	68.9	73.2	
Mean distance of cones in μ		14.7	13.9	9.8	13.3	12.7	10.5	9.9	11.3	12.0		11.7

Specimen	Body length	1	2	3	4	5	6	7	8	9	Mean number	Mean distance
21	15.3	—	37	71.5	44.5	—	54	68	64.5	38	53.9	13.5
22	16.5	32	41.5	65	32.5	29	53	54	66	76.5	49.9	14.3
25	16.5	23	24	66.5	30.5	33	61.5	66.5	44.5	38	43.1	15.2
Mean number of cones		27.5	34.2	67.7	32.5	31	56.2	62.8	58.3	50.8	49.3	
Mean distance of cones in μ		19.1	17.1	12.1	17.5	18.0	13.3	12.6	13.1	14.0		14.3

  The cones are distributed more densely in the center or bottom of the eye (Table 6) and in the outer or back part of the retina than the other parts. Hence they are smaller in size than the other parts. With the growth of fish the cones in a definite area of the retina decrease in number and increase in size. The mean distance of cones in the whole retina vary from 10.0μ, 11.7μ and 14.3μ correspondingly with the size of fishes 9.4—10.8 cm, 12.3—13.9 cm and 15.3—16.5 cm.

  In Table 7 is shown the density and the mean distance of cones in the central

Table 7. The number and mean distance of cones in $\overline{93\mu}^2$ in the central (3) and back (outer 6, 7) part of retina.

Specimen	Body length in cm	Part of retina			Mean
		3	6	7	
a	10	168.5	141.5	154	154.5
b	10	109	173.5	175	152.5
c	10	135	151	108	131.3
i	10.3	120.5	141	100	120.5
h	10.3	128	186.5	151	158.5
d	10.4	137	147.5	162	148.8
f	10.4	150.5	127.5	135	137.7
B	10.4	163	182.5	157.5	167.7
k	10.8	102	128.5	128	119.3
l	10.8	107	119.5	105	110.5
Mean number of cones .		132	150	138	140
Mean distance of cones in μ calculated from $d = 99.93/\sqrt{n}$		8.7	8.2	8.5	8.4

and the back part of the retina where the density of cones was highest (3, 6, 7 in Fig. 7 I) of such size of fish as used in the experiment (10—11 cm long). In these parts of the retina there existed 140 (n) cones in $\overline{93\mu}^2$ area and mean distance of them was 8.4μ. In Tables 8, 9 and 10 the relation between the density of the cones and the ganglion cells directly connected with the cones is shown as the result of measurement of the dissected materials. This relation is shown in Fig. 7 II, III. In the central (3) and the rear adjacent region (7), the number of cones per 1 ganglion cells is minimal (II in Fig. 7) or the number of ganglion cell per 1 cone is maximal (III in Fig. 7).

Table 8. Number of cones in $\overline{93\mu}^2$ area in different parts of the retina.

Specimen	Body length in cm	Part of retina								
		1	2	3	4	5	6	7	8	9
C	9.4	76	93.5	156.5	90.5	100	141.5	171.5	80	114
N	10	61	80.5	134.5	87.5	96	136	175	121	91
Q	10.3	74.5	63.5	121.5	80.5	80	109.5	92.5	82.5	85
R	10.3	57	70.5	119.5	81.5	80.5	173.5	108	115.5	102.5
B	10.4	58	79.5	163	77	72.5	182.5	157.5	86	87.5
P	10.4	64	67	130.5	78	87	154.5	165	115	135.5
A	10.8	58	55	85	80.5	82	141.5	133	86	86
G	10.8	83.5	68.5	119	86.5	75.5	115	123.5	84.5	76.5
W	10.8	67.5	54	107	73	73.5	119.5	100.5	102.5	84.5
J	12.5	50.5	54.5	136.5	60.5	62.5	82.5	88	68.5	63
I	13	45	52	102.5	64	51	86.5	122	83.5	69

Table 9. Number of ganglion cells in $\overline{93\mu}^2$ area in
different parts of the retina.

Speci-men	Body length in cm	Part of retina								
		1	2	3	4	5	6	7	8	9
C	9.4	33	46.8	94	35	39.4	75.6	135	41.1	47.3
N	10	31	34	94	30	36	65.9	94	70.5	47.3
Q	10.3	30.2	33	85	36.8	26	52	49.5	40.5	33
R	10.3	27	36	101.7	49.5	24.3	70.5	88.5	54	42.3
B	10.4	24.1	23.5	117.5	31.5	25.5	91.3	104.7	45.3	35.4
P	10.4	—	—	103	28.8	28	70	126	65	56.3
A	10.8	31	27	70.2	28	33	78.8	98	45	30.2
G	10.8	30.8	30.8	77.3	50.6	29.4	49.9	81	36.1	37.8
W	10.8	25.5	31.5	63	34	25.1	57	69.8	45	32
J	12.5	21.7	24.6	96	27.5	27	44.4	54.3	29.2	29.5
I	13	22	23	64	25	23	42	90	43.5	22

Table 10. Ratio of the number of cones/ganglion cells in
different parts of the retina.

Speci-men	Body length in cm	Part of retina								
		1	2	3	4	5	6	7	8	9
C	9.4	2.30	1.56	1.66	2.59	2.54	1.87	1.26	1.94	2.61
N	10	1.97	2.37	1.43	2.91	2.67	2.06	1.86	1.72	1.92
Q	10.3	2.47	1.91	1.43	2.18	3.08	2.10	1.87	2.04	2.55
R	10.3	2.11	1.96	1.17	1.65	3.30	2.06	1.22	2.14	2.42
B	10.4	1.78	2.41	1.39	2.44	2.84	2.01	1.50	1.90	2.47
P	10.4	—	—	1.26	2.71	3.10	2.21	1.31	1.77	2.41
A	10.8	1.87	2.04	1.21	2.87	2.71	1.81	1.36	1.91	2.85
G	10.8	3.75	2.23	1.54	1.73	2.57	2.30	1.52	2.34	2.03
W	10.8	2.65	1.71	1.70	2.15	2.93	2.07	1.44	2.28	2.64
J	12.5	2.33	2.22	1.42	2.20	2.31	1.86	1.62	2.34	2.14
I	13	2.05	2.26	1.60	2.56	2.22	2.06	1.35	1.92	3.14
Mean		2.33	2.07	1.44	2.36	2.75	2.07	1.48	2.03	2.47
Reciprocal of the mean		0.43	0.48	0.69	0.42	0.36	0.48	0.68	0.49	0.41

Although there is morphologically no clear Fovea in this fish, there is a region of relatively broad extension where the image of external object should be formed most accurately compared with the other regions of the retina as shown in II, III of Fig. 7. It is an interesting fact that such an accurately seeing region should be located in the central and rear adjacent region of the retina. The minute structure of the retina is so constructed that the fish is able to see accurately the front part of the head.

V. Change of Visual Acuity with Age

The resolving power of the eye increases with the growth of lens and decreases with the enlargement of adjacent cones distance. A smaller fish has a small eye i. e. small lens, but it has small condensed cones. With the growth of fish the lens increase in diameter but the cone in the retina becomes larger and hence the distance of each cone is enlarged. The change of the visual acuity of fish with age can be tested experimentally, but in this report this point has been made clear morphologically by the measurement of lens diameter and the mean distance of cones (Table 11).

Table 11. Relative visual acuity (S) of the fish calculated from the radius of lens and from the mean distance of cones. The number in bracket denotes the number of specimen.

Body length in cm	Mean radius of lens r in mm	$F=2.54r$* in mm	$F+r=3.54r$ in mm	Mean number of cones in $\overline{93\mu}^2$ n	Mean distance of cones $d=\dfrac{99.93}{\sqrt{n}}\mu$	$1/d$	Relative visual acuity $S=\dfrac{1}{\omega'}=\dfrac{F+r}{d}$
4– 5	1.18 (2)	3.00	4.18	190 (3)	7.25	0.138	0.58
5– 6	1.22 (6)	3.10	4.32	180 (6)	7.35	0.136	0.60
6– 7	1.36 (7)	3.45	4.81	179 (7)	7.46	0.134	0.65
7– 8	1.52 (1)	3.86	5.38	168.5 (2)	7.69	0.130	0.70
8– 9	—	—	—	147.5 (2)	8.25	0.121	—
9–10	2.09 (7)	5.23	7.29	149 (4)	8.19	0.122	0.89
10–11	2.26 (7)	5.74	8.00	137 (7)	8.54	0.117	0.94
11–12	2.49 (2)	6.32	8.81	115 (1)	9.34	0.107	0.94
12–13	2.52 (2)	6.40	8.92	103 (2)	9.89	0.101	0.94
13–14	2.70 (5)	6.86	9.56	94.5 (2)	10.3	0.097	0.93
14–15	3.23 (1)	8.20	11.43	—	—	—	—
15–16	3.34 (1)	8.39	11.73	62.5 (2)	12.6	0.079	0.93
16–17	3.55 (3)	9.02	12.57	61 (2)	12.8	0.078	0.98

* For spherical lens $F=\dfrac{n_2 r}{2(n_2-n_1)}$, $n_1=1.339$, $n_2=1.668$; then $F=2.54r$.

Morphological visual angle (ω') is given by the formula $\omega'=\dfrac{\text{mean distance of cones}}{\text{length of the eye axis}}=\dfrac{d}{F+r}$ The relative visual acuity (S) of the eye is given as $S=1/\omega'=(F+r)/d$, and is calculated in Table 11. The mean distance of cones was measured in the regions 3, 6 and 7 as in Fig. 7 I, where the density of cones was greatest. The lens diameter was directly measured from fresh material. The eye axis was calculated by r, as $F+r=2.54r+r=3.54r$. For spherical lens $F=n_2 r/2(n_2-n_1)$, $n_1=1.339$ (for sea water) and $n_2=1.668$ (from Table 5); then $F=1.668r/2(1.668-1.339)=1.668r/0.658=2.54r$. As shown in Fig. 8, the visual acuity of this fish increases with age becoming practically constant when the length of the fish reaches 10 cm so that the fish in maturity obtains a more accurate image of outer world than the young immature ones.
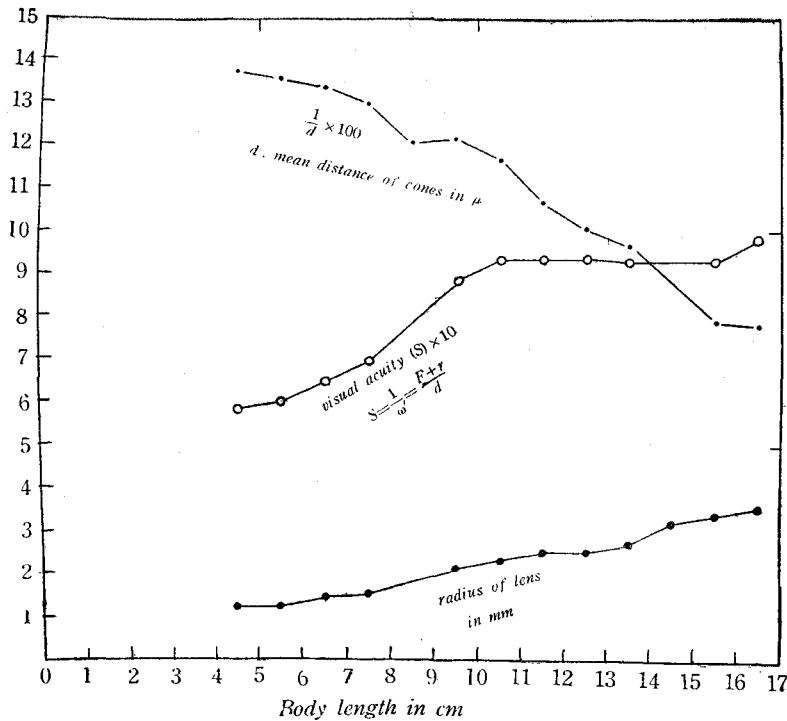
Fig. 8.   Change of visual acuity with age.

— · — · —   reciprocal of the mean cone distance.

— ● — ● —   radius of lens.

— ○ — ○ —   relative visual acuity (*S*).

VI.   Figural Transposition

a)   *When unexperienced equally striped figures presented.*

After the fish had been trained to the choice of a vertically striped figure of No. 12 (width of black or white line 0.34 mm) as against a horizontally striped figure, figure set No. 1 (width of each stripe 3.6 mm) was presented and the fish took bait from the vertically striped figure in spite of the coarser pattern.

b)   *When unequally striped figures presented.*

The fish had been trained to choose the horizontally striped figure No. 12 (width of stripe 0.34 mm).   After this training, both the horizontally striped figure No. 1 (width of stripe 3.6 mm) and vertically striped figure No. 12 (width of stripe 0.34 mm) were presented for free choice.   The fish chose the rougher striped horizontally striped figure.   After this test the relation of the above both figures was reversed (that is, horizontally striped figure No. 12 and vertically striped figure No. 1 were presented). The fish chose the originally trained horizontally striped No. 12 figure.   Further tests

of the same kind and in other figural combinations were carried out with principally the same results. It is clear that, in addition to accurately seeing the striation, the fish were able to distinguish the vertical and horizontal relation of the figural pattern.

c) *Absolute and relative selection.*

Three sorts of vertically striped rectangular figures 7×7 cm were prepared (Fig. 9). Five fish had been trained to choose the finer stripe II $(+)$ against the rougher I $(-)$. After training, figures II and III were presented for free choice. Next the same group
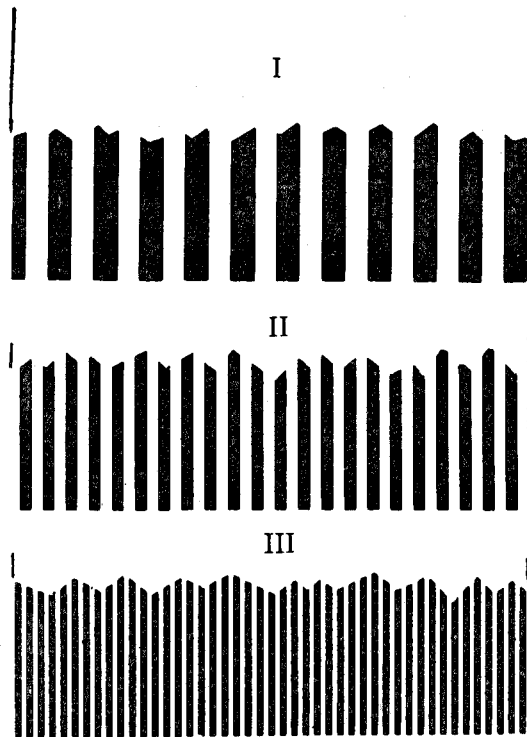
Fig. 9. Lower part of three vertically striped figures
$(7 \times 7$ cm$)$.

of fish were trained with figures II $(+)$ and III $(-)$. As a test figures I and II were presented.

The two figures were hung in sea water closely side by side. The same eatable bait was attached to the ends of wires hung just in front of the figural centers. At the outer side of each figure, a movable wooden plate was prepared, and when the fish had dashed to the negative or prohibited figure, the wooden plate was suddenly slid by experimeter's hand before the prohibited figure to discourage the fish taking the bait from the negative figure. When the fish took the bait before the positive figure nothing was done.

Such training was continued from 200 to 400 times over a period of 20 days. At intervals tests were made with a new pair of figures leaving the fish to free choice of the figure.

Table 12. Trained with the figures I ($-$) and II ($+$). Test was made with figures II and III. The number indicates the case of relative selection in 10 tests, that is, 10 indicates 10 choices of III, and 0 indicates no choice of III, or 10 choices cf II. 5 indicates 5 choices of III in 10 tests.

No. of fish	Number of III selection in test within the trained number of cases			
	Within 100 training	200	300	400
A	8	10, 8	—	—
B	2	1	5, 3	—
1	5	2	4, 7	5
2	4	5	—	—
3	4	3	0	2

Table 13. Trained with figures II ($+$) and III ($-$). Test was made with figures I and II. The number indicates the case of relative selection in 10 tests. 7 indicates the selection of I seven times in 10 tests.

No. of fish	Number of I selection in test within the trained number of cases			
	Within 100 trainings	200	300	400
A	—	3, 2	5, 0	5
B	9	5, 5	6, 5	—
1	7	5	5	5
2	—	7	5	6, 6
3	7	6	6, 5	—

Table 14. Arranged from the Tables 12 and 13. Evaluation of the selection numbers given in the above two tables. 0—3 absolute selection (a), 4—6 absolute and relative selection (a, r), 7—10 relative selection (r).

	No. of fish	Within 100 trainings	200	300	400
From the Table 12	A	r	r	—	—
	B	a	a	a, r	—
	1	a, r	a	a, r	a, r
	2	a, r	a, r	—	—
	3	a, r	a	a	a
From the Table 13	A	—	a	a	a, r
	B	r	a, r	a, r	—
	1	r	a, r	a, r	a, r
	2	—	r	a, r	a, r
	5	r	a, r	a, r	—

(continued)

relative	4 (50%)	2 (20%)	—	—
absolute, relative	3 (37.5%)	4 (40%)	6 (75%)	4 (80%)
absolute	1 (12.5%)	4 (40%)	2 (25%)	1 (20%)
Total cases	8 (100%)	10 (100%)	8 (100%)	5 (100%)
* Relative percentage	69%	40%	37.5%	40%
* Absolute percentage	31%	60%	62.5%	60%

* The percentage of absolute and relative cases (a, r) was divided by 2, and each
    numerical value was added to either the absolute cases or the relative cases.

Although the individual difference was great and the fish seemed in some cases
to choose the figure by temperament, the general tendency of relative selection at
first and of absolute selection later on with the progress of further training can hardly
be denied.

VII. Interpretation

When such a fish as *Microcanthus strigatus*, whose minimal visual angle is $4'23''$,
approaches a fishing line of 0.08 mm in diameter, the drail would be just found by
fish at the distance of 6.3 cm if the drail is dark colored and non-transparent. If the
fish has just found the drail at x cm from it, x can be calculated as follows:

0.08 mm$/x$ cm $= tg$ $4'23'' = 0.001275$, then $x = 0.08$ mm$/0.001275 = 6.3$ cm. The visual
angle of the drail at 5 cm distance is 0.08 mm$/5$ mm $= 0.0016$ or $5'30''$. The fish whose
minimum separabile is $4'23''$ can easily find such a drail at 5 cm. To make a fishing
line invisible to fish sight, man has by traditional experience devised fine, colorless
and transparent fishing lines. On the other hand easily visible thick threads or sticks
are used for fish weir, traps and barrier so as to let fish swim to a definite direction
or place.

When such a fish having lesser visual acuity than *M. strigatus* (minimum
separab. $4'23''$), for instance, *Phoxinus laevis* (minimum separab. $11'$) approaches the
finest drail of 0.08 mm in diameter, the fish would scarcely perceive the drail even if
it were colored and non-transparent, for the reason as such that the minimal visual
angle of $11'$ is reached first at the distance of 2.5 cm from the drail and that at such
a short distance no clear image of an object would be formed on the retina of fish.

The curve indicating the relation between visual acuity and light intensity in
man is sigmoid-formed (Fig. 10 I, KÖNIG, 1897). That of *Microcanthus strigatus* is
continuous double sigmoid-formed Fig. 4, Fig. 10 III). That of *Phoxinus laevis* shows
a brick point at low light intensity with a steep curve directed downward from it
(Fig. 10 II, BRUNNER 1934). The double sigmoid form of visual acuity curve plotted
in Fig. 4 and Fig. 10 III represents without doubt the functional difference of rods and
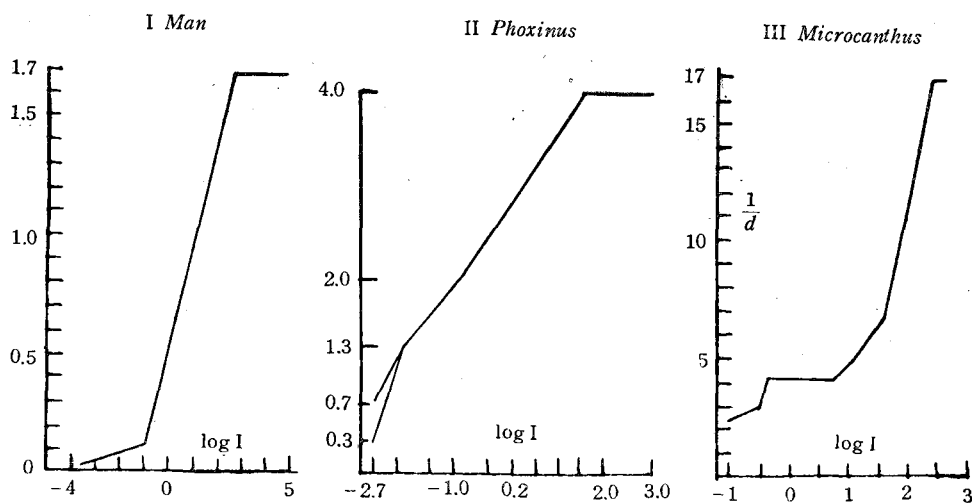cones in night and day vision of fish, as already pointed out by FRISCH (1924).

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Fig. 10. Visual acuity curve under different illuminations. Ordinate—value of visual acuity, abscissa—log of Lux. I after KÖNIG 1897, II after BRUNNER 1934, III deformed from Fig. 4.

Table 15. The site of transition of the function between rods and cones.

Animal	Site of transition	Author
man	0.03 ...0.1 Lux	KÖNIG 1897
,,	0.1......1 Photon	HECHT et WOLF (after BUDDENBROCK 1952)
Rana temporaria	about 2 Lux	BIRUKOW 1937
sword-tail	0.1......1 Milliambert	CROZIER et WOLF 1938
Phoxinus laevis	0.002...0.008 Lux	BRUNNER 1934
Microcanthus strigatus	0.4......5 Lux	in this work

Table 16. Minimal morphological and physiological visual angle of different animals.

Animal	Minimal morpholog. visual angle	Minimal physiolog. visual angle	Author
man	18.5–74″	23.3–64″	after BIRUKOW 1937
rat	—	30–57′	LASHLEY 1932
lizard (area)	3′06″	—	EHRENHARDT 1937
(periphery)	12′07″	11′28″	
pigeon	—	2.7–3.1′	HAMILTON 1933
game cock	—	3.1–4′	JOHNSON 1914
Rana temporaria	6′48″	6′53″	BIRUKOW 1937
Phoxinus laevis	11′	11′	BRUNNER 1934
Microcanthus strigatus	3′36″	4′23″–6′35″ average 4′59″	in this work
honey bee	1°	1°	HECHT et WOLF 1929
Drosophila	4°	4°	GRAVEL (after BIRUKOW 1937)
	4°	9.28°	HECHT et WALD 1934
hermit-crab	1.75–3°	4.2°	BRÖCKER 1935
Uca pugnax	2.05°	3.87°	CLARK 1935

Visual acuity increases in proportion to the size of eye, and is inversely proportional to the distance of each cone. Let Sm and Sp denote visual acuity of *Microcanthus* and *Phoxinus* respectively, and dm, dp the cone distance in μ, and Mm, Mp the length of eye axis respectively ($dp=6.25\mu$ BRUNNER 1934), then

$$\frac{Sm}{Sp}=\frac{Mm}{dm}\cdot\frac{dp}{Mp}=\frac{8\text{ mm}}{8.4\mu}\frac{6.25\mu}{2\text{ mm}}=2.93$$

When visual acuity is compared in term of minimal morphological visual angle ($\omega'm$, $\omega'p$), then

$$\frac{\omega'p}{\omega'm}=\frac{11'}{3'36''}=\frac{11'}{3.60'}=3.05$$

When minimal physiological visual angle is compared,

then
$$\frac{\omega p}{\omega m}=\frac{11'}{4'23''}=\frac{11'}{4.38'}=2.51$$

Minimal morphological visual angle should be theoretically smaller than the minimal physiological visual angle, as the incident light refracts strongly in the eye medium. Minimal morphological visual angle ($11'$) given by BRUNNER (1934) for *Phoxinus laevis* seems to be too high in comparison with minimum separabile ($11'$) from the above consideration. From (10) $\omega'=\frac{n_1}{n_2}\omega$, then when $n_1=1.333$ (for fresh water) and $n_2=1.668$ (from Table 5).

$$\omega'=\frac{1.333}{1.668}\cdot11'=8.80',\quad \omega'p/\omega'm=8.80'/3.60'=2.44$$

This value does not seem to be very far from 2.51.

From these comparisons, *Microcanthus strigatus* seems to have a 2 or 3 times keener vision than *Phoxinus laevis* as the eye size of both fishes suggests ($Mm/Mp=8$ mm/2 mm). In short, the difference in visual acuity between the two species of fish has been reasonably explained from the physiological and morphological points of view.

The following numerical values were found in *Microcanthus strigatus* of 10—11 cm in size:

ω, minimal physiological visual angle $4'23''$ $\cdots$ (1)
ω_1', minimal morphological visual angle deduced from (1) $3'30''$ $\cdots$ (10)
ω_2', minimal morphological visual angle calculated from measurement $3'36''\cdots$ (12)
d_1, mean distance of cones calculated from measurement 8.4μ $\cdots$ (7)
d_2, mean distance of cones calculated from experimental data 8.2μ $\cdots$ (11)
m_1, length of the eye axis measured 7.6—8.4 mm in average 8.0 mm
m_2, length of the eye axis calculated from $m=F+r=3.54r=8.0$ mm (Table 11)

though there is a small discrepancy in numerical value between ω_1' and ω_2', and also between d_1 and d_2, the general tendency of coincidence in paired values calculated or measured independently of each other can hardly be denied. The total lens refraction index ($n_2=1.668$) should be estimated as the proper value for marine fish on account

of the coincidence of the directly measured eye axis length with that of the calculated.

In some fishes the existence of Fovea has been demonstrated, for instance in *Siphonostomum typhle* and in *Hippocampus hochgradig* (OPPEL 1914, p. 73). *M. strigatus* has no clear Fovea, but in its retina there is the region of densely populated cones in the central and adjacent backward (outer) part of the retina surrounding processus falciformis (Fig. 7). This region would be estimated as actual Fovea. The adequacy of such microstructural differentiation in the retina has already been touched in the chapter III.

The visual acuity of fish is directly related with the net work of visual cells in the retina, and is not necessarily directly related with the distribution of ganglion cells as BRUNNER (1934) pointed out. Notwithstanding of this, there is, however, a close relationship between cones and ganglion cells so that in the actual foveal region of the retina the number of ganglions pro cone is highest in comparison with other regions of the retina (Table 10). Therefore it may be concluded that the visual acuity of fish is closely, though not directly, related with the distribution of ganglion cells.

HERTER (1929) has demonstrated the relative selection in figural transposition in *Phoxinus laevis* by training the fish to the series of grey paper. MÖRMANN (1934) was of the opinion that honey bee selected figures in relative direction in light and dark shade training, when training number was in medium, and that the honey bee had the tendency to select the figure absolutely when the training was continued many times. *Microcanthus strigatus* exhibited, however obscure, the same attitude towards figural transposition (Table 14) as honey bee, though in the former case striped patterns were used as the training figure.

VIII. Summary

1. The minimal width of striation of a striped pattern discriminated by the coral fish *Microcanthus strigatus* of 10—11 cm in body length, were 0.051—0.077 mm, in average 0.058 mm. 3 fishes among 4 discriminated 0.051 mm width in bright light. The visual angle of these widths seen at 4 cm from the figures were $4'23''$—$6'35''$, in average $4'59''$ respectively. The fish was able to discriminate the striped pattern at 4 cm from the figures relatively independently of the width of striation.

2. The visual acuity curve plotted against the log of illumination (Lux) exhibited a continuous double sigmoid form. The functional difference between rods and cones in day and night vision has been clearly demonstrated by this curve.

3. The total refraction index of spherical lens of fish was calculated ($n_2 = 1.668$) from $n_2 = \dfrac{2.678(m-r)}{2m-3r}$ by the measurement of the lens diameter ($2r$) and the length of eye axis (m).

4. The mean distance of two adjacent cones was calculated by counting the number of cones in a definite area ($93 \times 93\mu$), and was estimated as 8.4μ in fishes of

10—11 cm body length. The density of cones was highest at the central and adjacent back part of the retina surrounding process falciformis. This region actually seems to be a Fovea, though no clear one could be found morphologically. In this region ganglion cells were more dense than in the other parts of the retina considering the ratio between the number of ganglion cells and the number of cones.

5. The mean distance of cones in the actual foveal area derived from the minimal physiological visual angle was 8.2μ which coincided practically with 8.4μ found independently by the measurement of cone distribution in the retina.

6. The minimal morphological visual angle calculated from minimal physiological visual angle was $3'30''$, whereas that of morphologically found by measuring the mean cone distance and the length of eye axis was $3'36''$.

7. The change in visual acuity was computated by calculating the visual acuity from the size of lens and mean distance of cones in the retina. The relative visual acuity increased with the growth of fish and approached a constant level when the fish size became 10 cm in length.

8. During the training of fish to vertically striped patterns of different fineness, the selection of test figures by fish was made at first to relative direction in the test of figural transposition, and later an absolute selection surpassed the relative one.

9. The reason why in angling a fine, colorless and transparent fishing line is commonly used, is made clear, and also the differences in visual acuity between fishes with large eyes and those with small ones was discussed on the basis of optical data.

Acknowledgment

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